

MORPHOLOGICAL AND BIOLOGICAL OBSERVATIONS
ON SOUTH AFRICAN PLANTS.

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(Read March 25, 1896.)

1. *A case of Peloria in a S. A. orchid (Disa patula ?).*

No order of plants exhibits such marvellous differences in the shape of their flowers as orchids do, and yet their structure is surprisingly uniform. In most orchids (and in *all* S. A. orchids) the flower is composed of three sepals, three petals alternating with the sepals, one stamen, and it has further a trimerous pistil. Of the three stigmata which one would expect, two are usually confluent and the third forms a peculiar structure called the rostellum. In these orchids the single stamen is always placed opposite the odd sepal, and the latter is originally always placed opposite the axis from which the flower springs.* There are a number of reasons, some of which will be found in the introduction to Mr. H. Bolus's 'Orchids of the Cape Peninsula,' why we may ascribe theoretically to the orchid flower two alternating trimerous whorls of stamens, of which only one stamen is actually represented in most orchids, namely, the odd one of the outer whorl, while a few orchids only, such as the species of *Cypripedium*, possess the two lateral stamens of the inner whorl.

A great many plants which normally exhibit irregular flowers sometimes produce regular or "peloric" flowers, and it is a peculiarity of these peloria that they frequently have the structure which one has theoretically ascribed to the normal irregular flower. I was, therefore, greatly interested when I found amongst some flowers of a *Disa* (*D. patula* ?), which Mr. R. Schlechter collected last year near Humansdorp, one which had exactly the same diagram as the one which had been theoretically constructed for orchids generally by Charles Darwin and others. Peloria amongst orchids are very common, and (as Mr. Bolus informs me) even in South Africa, but such a theoretically nearly perfect case has not been put on record from this part of the world, and I may, therefore, be allowed to

* The diagram on p. 76 in Bolus's 'Orchids of the Cape Peninsula' ought to be reversed, in accordance with the usual practice of having at the top in such a diagram the parts nearest the parent axis.

describe it briefly. In justice to Mr. Schlechter I must mention that he recognised the peloric nature of the flowers handed to me, and that he asked me to investigate them.

In the genus *Disa* "the sepals * are nearly equal in length, free ; the odd one usually posticous, more rarely anticous, galeate, vaulted or nearly flat, spurred, saccate, or umbonate." In the flower which I am describing they were nearly equal in size, all of them were hooded and saccate (Plate I, Fig. 1 D), the odd one was anticous. "The petals [in this genus] are very various in shape, usually much smaller than the sepals." In our flower they were small linear structures (Fig. 1 C), concave on their inner sides, all of them were again of about the same size, and a "labellum" was, therefore, not observable. There was a distinct column which was free from the foliar structures just mentioned. It bore three stamens of equal size and proportions (Fig. 1 A st), alternating with the petals. Alternating with these, and therefore opposite the petals, there followed three more or less cuneate structures, which I take to be staminodes (Fig. 1 A st'). Although no pollen was, even in its initial stages, formed in them, their appearance would have reminded any botanist at once of stamens, and I think that my interpretation of these structures will not be challenged. In the centre of the column a rounded triangular protuberance could be distinguished. It was somewhat depressed in the centre and raised slightly towards the three corners of the triangle. These latter alternated with the structures which I have called staminodes, and I have no hesitation in considering the three raised portions of the central part of the flower as stigmata (Fig. 1 A stg). It will be seen at once when glancing at my sketch of this flower (fig. 1 A), which represents it with all parts spread out, that if my interpretation of its various parts is correct, it has the theoretical structure of an orchid flower. As all three stigmata are equally developed, a rostellum is, of course, absent. Whether they could have become functionally active is not in my power to decide, especially as the flower was still young, and a normal flower of corresponding age would probably not have been ready yet to discharge its pollen, even if circumstances had been favourable. It will be noticed in my sketch that the pollen sacs were tailed at the lower end, and it is perhaps worthy of mention that pollen was contained even in these tails. There was no sign of the eventual formation of caudicles, and none of the stigmata showed any peculiarity indicating the formation of the glands normally formed on the rostellum, the function of which is to provide a sticky substance for the removal of the pollinia by the agency of insects.

* The passages in inverted commas are taken from Mr. H. Bolus's 'Orchids of the Cape Peninsula,' p. 134.

The question naturally arises whether the flower I have described represents a case of atavism, a reversal to an original type. I will, however, not venture on any speculation on this subject, for on the two spikes which I had at my disposal there were some flowers which resembled the one which I have described, but were not quite so regular, and did not possess any staminodes, but there were also several with a different structure. They had a floral envelope composed of two alternating whorls, each composed of two hooded and saccate structures similar to the sepals of the flower first described; they had four stamens equally well developed as the stamens of the first flower, and they had (I believe) two stigmata.* Here we have, therefore, orchidaceous flowers which are dimerous right through. I think it right to put these cases on record, but I do not feel justified in drawing any conclusions from the facts which I have ascertained.

2. *The structure of the flower and the method of pollination in Crassula canescens*, Schult.

The following observations were made on plants grown in my garden at Grahamstown, within about half a mile from a spot where the species is growing in its wild state.

Crassula canescens, Schult., belongs to the section *Globulea* which is characterised in Harvey and Sonder's 'Flora Capensis' as having panduriform petals which bear an oblong or ovate fleshy "gland" immediately behind the blunt apex. I do not know what has led to the belief that the knob-like structures on the petals are glands, but I may state at once that they are not excretory organs, and for want of a better term I will call them "epipetalous knobs." I have reason to believe that in the other species of *Cassula* § *Globulea* these knobs are in structure and function similar to those of *C. canescens*.†

The peduncle of *Crassula canescens* is scape-like, and bears a few densely capitate cymules. The appearance of the epipetalous knobs, which are white, announces the time when the flowers are ready to be fertilised; before this time they are, with the rest of the corolla, enclosed by the calyx. As soon as this stage is reached the flowers are plentifully visited by a hymenopterous insect (*Synagris emarginata*, Sauss.?) ‡ A dissection of the flower does not show any appreciable quantity of nectar, but when covering up a cluster of flowers

* I could not be quite sure about their number.

† This is certainly the case in *C. radicans*, Haw, *C. cultrata*, L., and *C. obvallata*, L. As regards structure of flower, insect visitors, and fertilisation, my remarks on *C. canescens* apply also to these species, as I was able to ascertain after writing the above account.

‡ Mr. L. Péringuey, who kindly tried to identify the insect for me, could not state its name positively as I could only send him a female.

with muslin for about a week I found afterwards a fairly copious supply of nectar in all flowers which had reached the stage above mentioned, and at the same time I noticed that the epipetalous knobs did not show any secretion whatever. Furthermore, by means of anatomical investigation I could not demonstrate in them any tissue that resembled the well-known excreting tissues of other vegetable glands. The nectar inside the flowers appeared to have been secreted by the small scale-like bodies, which in this plant, as in the majority of crassulaceous plants, are found at the bases of the carpels on their outsides. It seemed to me, therefore, certain that the above-mentioned insects came to the flowers for the purpose of sucking nectar, and it seemed, further, most probable that they were the means of effecting the pollination of the plant. I may mention that no other insect was observed visiting the flowers, and that *Synagris emarginata* (?) seemed to prefer *C. canescens* although, I believe, it occasionally also visited (after exhausting all flowers of the *Crassula*) flowers of mignonette,* which were growing in profusion close by. The five egg-shaped epipetalous knobs of each flower are, as stated above, seated behind the portions of the petals which appear to be their true apices, and when they have made their appearance it looks as if the flower had opened. However, as a matter of fact, *the flower never opens*. To explain this more clearly I must give a short description of a petal, which will, moreover, help to explain some of the remarks which I have to make further on. It can easily be seen that each petal is thickest along the median line (Plate I, Fig. 2 A), and that it flattens out towards both its sides—one might almost say that it has a kind of midrib with broad wings. In making a median longitudinal section (Plate I, Fig. 2 C) through a petal it will be observed that the “epipetalous knob” forms the natural continuation of this midrib, and thus forms the true apex of the petal. The small, thin projection of the petal at the base of the epipetalous knob, which has hitherto been considered the apex of the petal, has, therefore, probably to be considered of the nature of a ligula,† but as I have not studied carefully the development of the petals I do not wish to insist too strongly on this interpretation. What concerns us here are two points—namely (1) each epipetalous knob is firmly connected with the thickest portion of the petal, and thus a lateral pressure on it, if sufficiently strong, will move the whole petal, and (2) the projecting thin portions of the

* I have since observed the same insect sucking nectar from the flowers of a *Euphorbia* at a time (May, '97) when no species of *Crassula* § *Globulea* was in flower.

† Similar ligular structures are found in *Boraginaceæ* where they frequently have the same function as in *Crassula* § *Globulea*.

petals close the entrance to the flower completely, and no access to it can be gained unless the petals are pushed apart and they themselves bent. Now it is by no means easy to push the petals apart, for we find that they are closely interlocked as they stand very close together, and are, moreover, imbricate (Plate I, Fig. 2 H p), but in addition to this they are closely surrounded by the comparatively thick sepals which have to be pushed aside at the same time. We can understand now that the entrance to the flowers is completely barred to small insects and all insects which have only soft mouth-parts. But a middle-sized hymenopterous insect, such as *Synagris emarginata*, with its wedge-shaped, hard mouth-parts, has no difficulty in gaining access to the flower. To these wedge-shaped, hard mouth-parts the epipetalous knobs form excellent points of resistance when the insect wants to prise a flower open and suck the nectar contained in it by means of its soft mouth-parts enclosed in the former. This is, as far as I can make out, their whole purpose in the economy of the flower.

The sepals and petals together form an elastic structure, so that the flower closes again immediately the insect has left it, and the same process has to be gone through again if another insect wants to gain access to the nectar.

Turning now to the sexual organs of the flower, we find that both anthers and stigmata are in the line which the mouth organs of the insect have to traverse to reach the nectar-producing glands (Plate I, Fig. 2 G gl). When examining the stigmata of a flower which shows the epipetalous knobs boldly, but in which the anthers have not opened yet, we frequently find germinating pollen-grains on them. Thus the stigmata are ready to receive pollen before the anthers of the same flower have discharged theirs. *The flower is protogynous.* Pollen germinating on the stigmata at this stage must have been brought from some other flower by the visiting insects, and *these insects, therefore, effect cross-fertilisation.* When the anthers open the pollen remains attached to them, but from their position it can be inferred that visiting insects cannot fail to brush some of it on their heads and carry it to the stigmata of the next flower which they visit. The stigmata remain receptive for a considerable period, and if the pollen of a flower is not removed part of it is deposited on the stigmata of the same flower. In flowers which were protected from insect visitors by a covering of muslin I found repeatedly large numbers of germinating pollen grains on the stigmata, and although I did not carry the experiment so far as to see whether these flowers would produce ripe seed, I think it is not far-fetched to conclude from the fact just mentioned that *self-fertilisation* is also possible.

3. *On some points in the morphology of Aizoaceæ.*a. The inflorescences of some species of *Mesembrianthemum*.

In a number of species of *Mesembrianthemum* the flowers are borne singly at the ends of vegetative shoots. This (judging from the illustrations in De Candolle's 'Plantes Grasses') is, for instance, the case in *M. spectabile*, *M. felinum*, *M. longistylum* and *M. glaucum*. The same appears to be the case in *M. lateriflorum*, only here the flowers appear at the end of short lateral branches bearing only two foliage leaves. In all these species the leaves have a decussate arrangement. In *M. brachiatum* and other species the leaves are also placed in pairs opposite one another, but the uppermost pair have branches in their axils which, after producing a pair of leaves, end in a flower. Thus a typical *dichasium* is the result. The two leaves preceding each flower can be considered as prophylls, and further branching often takes place with the same result, and thus the dichasial formation of the inflorescence is continued.

In some other species, such as *M. cordifolium* (Plate II, E) *M. helianthoides*, *M. viridiflorum*, *M. crystallinum* and *M. angulatum*, the inflorescences appear at first sight to be very different from the simple cases just cited, but on careful examination it will easily be found that the formation of their inflorescences is essentially the same. It is certainly so in their youngest stages, except that the corresponding branches are not equally strong from the first, and only later on their behaviour becomes different.

In *M. cordifolium*, which I have examined in the live state, there are two equally well-developed branches formed in the axils of the two leaves preceding the terminal flower of a vegetative shoot. Each of these bears two leaves and ends in a flower. In the axil of each of these leaves a bud is formed, but only one of them develops strongly at first, and its axis places itself into the prolongation of its parent axis, throwing the terminal flower (Plate II, E II) aside. Thus a sympodium, or false axis, is formed, and as the favoured side-branches proceed alternately from the right and left side of the relative main axis the inflorescence is, if we only take these branches into consideration, a *cicinnus*, but it is not quite pure, as the opposite branches also develop later on and produce a flower after forming two leaves, and thus a true *dichasium* is formed, which, however, through the formation of the sympodium, is obscured. There is no term in the English language to adequately represent this form of inflorescence; in German it is called a "dichasium mit wickeltendenz." *M. helianthoides* appears to agree in the points just mentioned with *M. cordifolium*.

The cases hitherto mentioned will assist us in understanding the

inflorescence of *M. angulatum*, which is even more complicated. This plant is a common weed in Grahamstown gardens. The seedling of *M. angulatum* produces a richly branched axis in which the leaves are decussate, but as soon as flowers are produced the leaves instead of being opposite appear to be alternate with divergence $\frac{1}{2}$. On the flowering branches we notice that the flowers are lateral (Plate II, D, I, II, III) and without bracts. We further see that every second leaf is opposite a flower (Plate II, D, β , &c.), and that, as a rule, the alternate leaf bears two branches in its axil (Plate II, D, α , &c.), the upper one being more strongly developed than the lower one. This latter we recognise as an accessory shoot, while the more strongly developed one may be regarded as the normal shoot of this leaf. The second leaf (Plate II, D, β , β' , &c.) bears in its axil a shoot in a similar state of development as the accessory shoot of the first leaf, and we may, therefore, without inquiring further at present, also regard it as an accessory shoot, while the axis of its normal axillary shoot has, as in *M. cordifolium*, placed itself into the prolongation of its parent axis and formed a sympodium. We thus see that here also the flowers are really terminal, and have only been thrown aside by the strong growth of a lateral axis. That this is not mere theory can easily be seen when the youngest parts of an inflorescence are examined. But in any case the inflorescence must be considered a true cincinnus if we leave the accessory shoots and the free lateral shoots out of account. In a cincinnus we must find that the branches composing it are produced alternately to the right and left of the main axis. In Plate II, A, in which I have represented the ground plan of part of the inflorescence of our plant, this will be clearly seen to be the case. In this diagram I have called the lower leaf of the two placed below each flower α , α' , α'' , &c., the upper ones being marked β , β' , β'' , &c. The organs seated on the sympodium are drawn black throughout, organs on normal "free" branches are outlined and those on accessory shoots are indicated by dotted lines. The size and shape of the sepals give us a ready means, even when they are full grown, to determine the order in which they have been formed. It can easily be seen that they are arranged in a spiral with a divergence of $\frac{2}{3}$. Taking any of the flowers (I in Plate II, A) as a starting-point, and looking at it by facing sepal No. 2 through the axis of the flower, we find leaf β on the right. This leaf has a shoot in its axil bearing two leaves, α' and β' , and terminating in flower II. Looking now through the centre of this flower at its second sepal, we find the next upper leaf, β' , to our left, and thus the sympodium

is continued by the shoot on the left side. Examining after this the shoot terminating in flower III, we find that the shoot continuing the sympodium is to our right, and the next one is to the left of its relative main axis, &c. By glancing at the sketch of an inflorescence (Plate II, D) and at the diagram which we have just considered, it will be seen that all flowers on the sympodium occupy one side of it (the upper side) but are arranged in a zigzag line, separated horizontally by an angle of 90° , while all β leaves occupy the lower side and are arranged similarly as the flowers. While we can thus trace a cincinnus with a sympodial axis composed of the shoots of β leaves starting from β of the first flower, we must not lose sight of the fact that, as in *M. cordifolium*, α also has an axillary shoot, which grows according to the same rules as the β shoot, and that thus the total inflorescence is again a dichasium, but as its axis cannot place itself into the prolongation of the parent axis it appears in its true colour as a lateral branch of the latter, but also develops according to the same laws as the axis on which it is seated. However, it will be seen that the branching from this shoot is much poorer than from β , and thus here also the inflorescence is a "dichasium mit wickeltendenz." I said before that between each normal shoot and its bract an accessory shoot may arise, and I have to add that, when it develops properly, its growth proceeds also on the same lines as the normal shoots.

It is a well-known fact that, as a rule, in dichasia corresponding shoots are antidromous. I know no clearer example illustrating this rule than *M. angulatum*. We will consider the shoots in the axils of α and β (Plate II, A). In the axil of the former we have a shoot bearing two leaves, α' and β' , and the flower $\text{II}\alpha$. As the leaves are opposite one another we cannot decide at first whether we have to connect them by a right or left spiral, but if we look at the sepals we see that these are arranged in a right spiral.* We also notice that if we try to pass from α' to β' and then to the first sepal by the shortest way, we have to turn in the same direction in which the sepals are arranged—we have to traverse a right spiral. On the other hand, we find that the leaves on the shoot in the axil of β can be seen to be arranged in a left spiral if we include the sepals of the flower $\text{II}\beta$. By looking at the sepals of flowers I and $\text{II}\beta$ we see that they are also antidromous, the sepals of I being arranged in a right spiral, those of $\text{II}\beta$ in a left spiral, and by comparing succeeding flowers on the sympodium we find that succeeding flowers of the

* A spiral which turns in the same direction as the hands of a watch is called by botanists a right spiral. A left spiral of course turns in the opposite direction.

sympodium are always antidromous, whereas the flower terminating the ill-developed "free" shoot is homodromous with the flower terminating its relative main axis. The result of the arrangements which I have described is such that all organs of the plant which require light get a maximum of it. Given the same forms of stems, leaves, and flowers, and the well-known straggling habit of *M. angulatum*, I doubt whether any other combination of these parts could secure to them more advantageous positions than they occupy in nature. A fuller consideration of this point, which is of the very greatest importance, I will leave for the present but hope to revert to it in some future paper.

b. The development of the flower in *Mesembrianthemum angulatum*.

There is nothing remarkable in the structure of the flower of this plant, except that the placentation remains permanently axile, whereas, as is well known, in a great many species of *Mesembrianthemum* the placentation, though originally axile, becomes parietal in the fully developed flower. My reason for studying the development of the flower of *M. angulatum* was chiefly to form an opinion of my own on the origin of the so-called petals in the genus. The result agreed entirely with the facts found by Payer and Hagen. The very numerous so-called petals and the stamens arise together from five protuberances or "primordia" (Plate II, B pr) after the sepals have made their appearance. These split up by a series of radial and concentric divisions, and the outer of them become the petals, whereas the inner ones develop into stamens (Plate II, C st). Strictly speaking, therefore, the so-called "petals" are staminodia, and the genus *Mesembrianthemum* is to be regarded as apetalous, as is now usually done by botanists. In our case the three outermost rows of serial structures resulting from the five primordia of the androecium develop into staminodes (Plate II, C st'), and as there are usually 30 radial series formed, their total theoretical number is 90. I counted 82 in one flower. As is usual in structures arising in close proximity to one another, some succumb to the pressure exercised by the others, and thus the smaller actual number may be accounted for. Altogether there are usually eight structures in each radial series—this would leave five for the real stamens, and their total theoretical number would be about 150.

The staminodes soon flatten out and overlap, but even in a full-grown flower one cannot help being struck with the similarity between the filaments of the proper stamens and the staminodes, and this similarity is greatest where the two adjoin, and from this fact one might also be led to the conclusion that the so-called "petals" are stamens without anthers, or in other words staminodes,

which, however, through the study of the development of the flower, becomes an absolute fact, and thus justifies us in uniting *Mesembrianthemum* with other truly apetalous plants, such as *Aizoon*, *Galenia*, &c., into one natural order, the *Aizoaceæ*.

c. The inflorescence of *Galenia spathulata*, Fenzl.

Galenia spathulata is a more or less prostrate herb which is also a common weed in Grahamstown gardens. When examining its flowering region, it appears at first sight as if here the universal axillary branching of flowering plants did not obtain. If we examine a strongly developed shoot, it appears as if its branches arise by the side of the leaves, and that, therefore, they are without bracts. But by comparing it with the inflorescence of *Mesembrianthemum angulatum*, we find that we have to deal here with a similar inflorescence, although it is different in some details. In *M. angulatum* we may assume that the β leaf adheres to its axillary shoot for some distance, and that in this way the ordinary decussate arrangement of leaves in the species of *Mesembrianthemum* is altered into the alternate arrangement which we meet with in its inflorescence. We may further assume that the axis of its axillary shoot adheres to the axis of its parent shoot up to this point. If, on the other hand, both α and β adhered to the axis of their axillary shoots for some distance while the axis of the parent shoot (bearing flower I) remained short, we should have an inflorescence exactly the same as that of *Galenia spathulata*. Here again the shoot in the axil of β is favoured in growth, and, throwing the terminal flower aside, places itself into the prolongation of the parent shoot. It will now be seen why the free shoot in the axil of α' is found by the side of β and separated from it by a angle of 90° , while α' is found as the first leaf *on* this free shoot. The ground plan of this inflorescence is exactly the same as in *M. angulatum*, and even the further complication in the latter, namely, the formation of accessory shoots in the axils of both α and β occurs not infrequently. Thus we find a further common feature between *Galenia* and *Mesembrianthemum* in the fact that even in these highly complicated inflorescences the design, so to speak, is exactly the same.

EXPLANATION OF FIGURES:—

PLATE I.—

FIG. 1.—*Disa (D. patula ?)*.

A. Peloric flower (magnified), all parts spread out. s=sepal, p=petal, st=stamen, st'=staminode, stg=stigma.

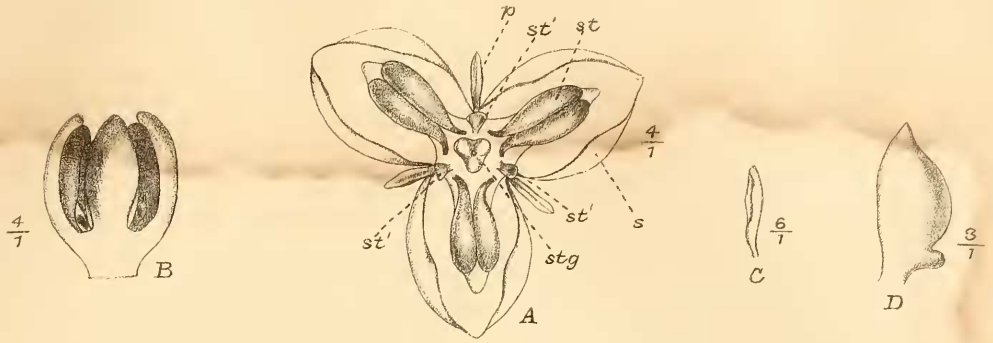


Fig. 1

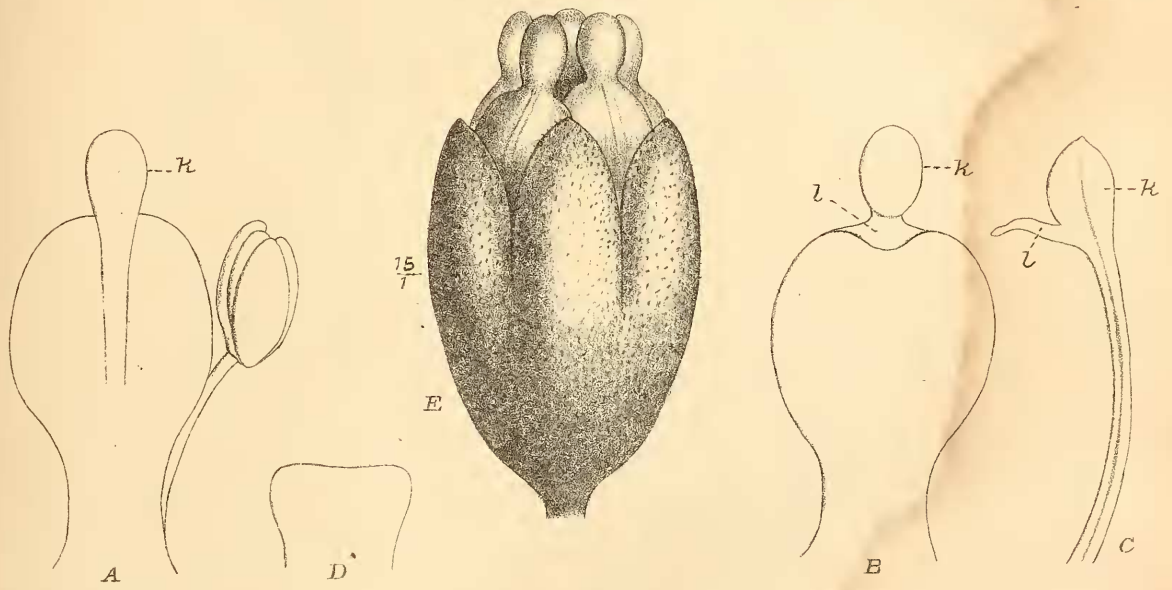


Fig. 2

